

outer marginal tooth, plus the marginal plate. The inner marginal tooth tends to be different in size from the outer marginal tooth, but similar instead to the lateral tooth.

Reduction and loss of the marginal plate is frequent in teuthoids. Unicuspid, bicuspid, and tricuspid rachidian teeth and unicuspid or bicuspid lateral teeth are seen in many groups. The shape of the inner marginal tooth is correlated with the function of compaction and support against stress of the outer marginal tooth.

Octopods differ in having the lateral tooth on each side reduced to a small remnant, the rachidian tooth enlarged—often with variable cusps, and, usually, a massive outer marginal plate.

Once the clear distinction is made between cusp-bearing teeth and the marginal plates, which function for erection, support against stress, or compaction (folding), or both, then much of the discussion concerning numbers of teeth in a transverse row in the Cephalopoda becomes irrelevant. The nautiloids do differ in having 9 teeth and 4 plates in each row, that is, an additional pair of lateral teeth and an additional pair of support plates over those found in typical coleoids. The coleoids characteristically have 7 teeth and 2 plates in each row, with the support plates reduced or lost in sepiolids and many oegopsid squids. Some gonatids have only 5 teeth per row. The inner marginal tooth of teuthoids is more modified than the outer marginal. Octopods generally are characterized by having a modified and enlarged rachidian, greatly reduced laterals, and very large marginal plates. Some cephalopods lack radulae altogether.

Thus the coleoids have rather limited variations on a basic plan, rather than showing the more radical differences implied by counting the outer plates as teeth or by overlooking the minute lateral tooth of most octopods. Some cephalopods, such as *Spirula* and cirrate octopods e. g., *Opisthoteuthis* (Solem & Roper, unpublished), totally lack a radula (see also ROBSON, 1932: 9).

A thorough discussion of the phylogenetic implications of the radula will appear in our later work. Although the

topic has been discussed in the literature (ROBSON, 1932: 7-12), no conclusions have been reached, nor is there agreement on which type of radula represents the primitive form. We do know, however, that the radula of nautiloid cephalopods is a very conservative structure that has persisted nearly unchanged in basic structure for about 300 million years (SOLEM & RICHARDSON, 1975). The radula in the orders of living coleoids also is similar in basic structure. The details of structure do vary at different taxonomic levels, even to the extent that some congeneric sympatric species have dissimilar radulae. The variations on the conservative structural plan of the radula appear to be an overlay imposed by the evolution of a variety of feeding characteristics throughout the cephalopods.

SUMMARY

A review of published scanning electron micrographs of cephalopod radulae, together with illustrations of the radula of *Loligo plei*, *Histioteuthis dofleini*, *Vampyroteuthis infernalis*, and *Octopus briareus* permit identification of different functions for marginal plates, clear distinction between teeth and plates, and clarification of the basic number and patterns of teeth and plates in major taxonomic categories. Marginal plates may function either to erect outer marginal teeth or to support them against stress. Nautiloid cephalopods differ from coleoids in having two extra lateral teeth and two inner marginal support plates. Coleoids vary in cusp patterns on the rachidian and lateral teeth, with the teuthoids varying from possession of strong marginal plates to their complete loss. Octopods are characterized by a greatly reduced lateral tooth, a very enlarged and usually multicuspid rachidian tooth, and massive marginal plates. *Vampyroteuthis* is unique among examined species in having an anterior prolongation of the rachidian that provides support against stress during feeding. The conspicuous grooves present on the teeth of many cephalopods function during compaction or infold-

Explanation of Figures 19 to 23

Octopus briareus Robson, 1929

USNM 574777; 24°38' N; 82°55' W; ML = 39mm

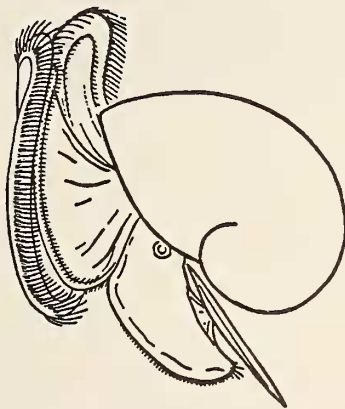
Figure 19: Part row of teeth	× 90
Figure 20: Anterior view of teeth	× 96
Figure 21: Rachidian teeth in lateral view	× 189
Figure 22: Cusp variation on rachidian teeth	× 189
Figure 23: Details of folding pattern of marginal teeth	× 194



ing of the teeth towards the midline of the radula. These grooves cause the outer teeth to "lock" down either on the support plates (*Nautilus*) or against the inner marginals and laterals (coleoids). When the outer marginal plates are greatly reduced or lost, the grooving on the teeth often is reduced or lost and a different pattern of tooth folding or erection, or both, is evolved. In some teuthoid taxa that lack marginal plates an entirely new structure is present, a marginal tooth ligament that extends from the anterior basal plate of the outer marginal tooth to either the basal membrane or the posterior part of the basal plate of the next anterior outer marginal tooth. This structure was not reported previously.

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Two Pleistocene Volutes from the New Hebrides

(Mollusca : Gastropoda)

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(2 Plates; 1 Text figure)

INTRODUCTION

IN 1973, DURING a search for road surface materials on the island of Santo¹ in the New Hebrides, D. I. J. Mallick and David Greenbaum of the New Hebrides Condominium Geological Survey made extensive collections of mollusks and other fossils from a series of loosely consolidated dark marls (SM242) lying about 70 m (230 feet) above sea level on the Kere River about 5 km inland. Mr. Mallick had previously located similar beds outcropping on the Navaka River (SM43) about 12 kms to the southwest at an altitude of 50 m (165 feet). Both localities are shown on Figure 1. The deposits appear to represent off-shore beds laid down at depths in excess of 50 m.

Some of the molluscan and crustacean fossils that were sent to the National Museum in Washington for identification proved so interesting that Thomas Waller of the Museum staff and Warren Blow of the U.S. Geological Survey decided to visit the sites to collect bulk samples. The first of the two new *Lyrias* here described was obtained by Dr. Mallick on the Kere River and is named for him. The second *Lyria* was collected by Waller and Blow from both the Kere River and the Navaka River outcrops.

LOCATION

SM43 Navaka River, Santo, New Hebrides
166°51.04' E, 15°36.08' S
Altitude 50 m (165 feet)
D. I. J. Mallick
(U.S. Geological Survey Cenozoic locality No. 25742 collected from boulders at north end of outcrop by

Thomas Waller and Warren Blow, June 1974).
SM242 Kere River, Santo, New Hebrides
166°56.74' E, 15°34' S
Altitude 70 m (230 feet)
D. I. J. Mallick (U.S. Geological Survey Cenozoic locality No. 25715 collected by Thomas Waller, John Bolango and Warren Blow, June 1974).

PALEOECOLOGY

The outcrops on the Kere and the Navaka Rivers have a number of molluscan species in common and are believed to be of essentially the same age. Detailed faunal analyses are as yet incomplete but it is apparent that the Kere River fauna contains a much higher percentage of large mollusks than the outcrops on the Navaka. Many of the large shells are species that live intertidally or at very shallow depths. The shells from both areas are exceedingly well preserved. They exhibit a natural polish and many from the Kere retain clear traces of their original color patterns. The total number of molluscan species exceeds one hundred. Ecologically both faunas are somewhat mixed.

The thousands of larger shells obtained by Messrs. Waller and Blow on the Kere River include more than 20 species of *Conus* and the cypraeids are also abundant. Many of the latter, like the cones, are thick shells. Numerous examples are heavily encrusted, both outside and inside, with barnacles, bryozoans, and a variety of calcareous tubes. Other shells are pierced by bore holes and some of the shallow water species have segments of *Halimeda* or other calcareous grains tightly wedged in their apertures. Neritids are represented in the Kere River collections by at least two species but all the shells are badly worn and/or fragmentary. With the robust shallow water types are fragile shells, including those of *Phenacovolva longirostrata*

¹ Formerly known as Espiritu Santo; the first word was officially dropped recently